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Patterns of acoustic phenology in an anuran assemblage of the Yungas Andean Forests of Argentina

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Abstract. Breeding seasons in anurans are usually noticed by their advertisement calls, which stand as the main signal emitted by males during their adult life. These calls are species-specific signals with multiple information and can be used to monitor anuran populations over extended time periods. Applying a Passive Acoustic Monitoring method (PAM), we described the acoustic breeding phenology of an anuran assemblage along an altitudinal elevation range in the Yungas Andean Forest of Argentina. In addition, we propose a new classification system for their acoustic phenological strategies, based on

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the male's calling records throughout an entire year. Also, we assessed the temporal and spectral niche overlap by the anuran species recorded. The assemblage was active throughout the entire year, with a higher concentration of calls recorded during the spring-summer season. We describe five distinct Acoustic Breeding Strategies based on the calling patterns of the recorded species. Temporal niche overlap was higher in the spring-summer season and in the lowest study site. The use of a PAM as a tool to monitor the advertisement calls in anurans communities could be a reliable technique to obtain different information about the species' acoustic phenology and the temporal use of the acoustic communication channel.

Keywords. Acoustic breeding strategies, acoustic phenology, advertisement calls, anurans, calling guilds, Passive Acoustic Monitoring.

INTRODUCTION

Advertisement calls are the main signals emitted by anurans during the breeding season (Wells, 2007). These species-specific features are mainly expressed by males, with some exceptions in females (e. g., the bullfrog *Lithobates catesbeianus*) of certain species, and voiceless males like *Rhinella gallardoi* (Emerson and Boyd, 1999; Carrizo, 1992). Advertisement calls are considered key factors for mate selection (Márquez and Verrell, 1991; Gerhardt and Huber, 2002; Wells and Schwartz, 2007) and are used by receivers according to their temporal and spectral characteristics, both for identification and location of their potential pairs, as well as to recognize the quality of the emitter (Gerhardt and Schwartz, 2001; Mason, 2007). Thus, these signals are used in mate choice behaviour, transmitting several messages simultaneously (Candolin, 2003). In addition, due to their

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"species-specific" nature, these are used as a taxonomic character for species description and identification (Köhler *et al*., 2017). Thus, advertisement calls have been widely used in long-term monitoring programs (Bridges and Dorcas, 2000; Dorcas *et al*., 2009; Llusia, 2013; Márquez *et al*., 2014; Measey *et al*., 2016). The surveying of advertisement calls has proven to be a useful technique for detection and monitoring of anuran species at large spatial scales (de Solla *et al*., 2006), as well as for assessing population changes over time (Buckley and Beebee, 2004; Pieterson *et al*., 2006). These kinds of surveys can also provide valuable information about threatened species that breed in narrow time windows or display sporadic calling activity (Williams *et al*., 2013; Willacy *et al*., 2015; Akmentins and Boullhesen, 2020).

The breeding phenology of anurans, monitored through their advertisement calls, can be explored at different time scales, mainly in regions where seasonality shapes the extent, the start, and ending of their breeding activity (Weir and Mossman, 2005). Thereby, different species may have distinct daily and seasonal calling patterns (Cook *et al*., 2011; Yoo *et al*., 2012). Studying these calling patterns, can serve as a tool to define the core calling periods of the species recorded (Lemckert and Mahony, 2008), for which it is considered of utmost importance to increase the detection probability in anuran survey programs. The use of automated recording devices for passive acoustic monitoring techniques (PAM) can add valuable information such as the acoustic breeding patterns, as several species of anurans may breed simultaneously in different reproductive sites (Nelson and Garcia, 2017; Duarte *et al*., 2019; Ulloa *et al*., 2019; Pérez-Granados *et al*., 2020).

Amphibians are suffering alterations in their phenological patterns because of the increasingly frequent extreme climatic events caused by the global climate crisis (Lanno and Stiles, 2020). This is particularly concerning for the species distributed throughout

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the biodiversity hotspot of the tropical Andes of South America (Myers *et al*., 2000), which are severely affected by the consequences of climate change (Burrowes, 2008). In addition, in times of the global diversity crisis, amphibians are considered the most affected groups among terrestrial vertebrates (Stuart *et al*., 2004; IUCN, 2023).

Based on the temporal pattern of their breeding phenology, anurans have been historically classified into two discrete groups, as proposed by Wells (1977): explosive breeders and prolonged breeders. Although there is a behavioural continuum between these two extremes (Wells, 1977; 2007). In recent years, several works focused on better describing the breeding acoustic strategies that can be found in anuran species (Chen *et al*., 2023; Donnelly and Guyer, 1994; Forti *et al*., 2022; Huang *et al*., 2001; Prado *et al*., 2005; Prasad *et al*., 2022; Bertoluci and Rodrigues, 2002) but there is still missing information mainly for Neotropical anurans. Continuous monitoring of anuran advertisement calls along different spatial-temporal scales, can provide valuable information about the different breeding strategies displayed by each species in an assemblage (Moreira *et al*., 2007).

The acoustic niche hypothesis (Krause, 1987) proposes that each individual elaborating messages through sound in each environment will present a partition in its spectral and temporal features, to avoid being masked by others (Krause, 1993). In species-rich assemblages from different clades, different strategies are expected to be present to avoid the competition in the acoustic communication channel (Bertolucci and Rodrigues, 2002; Herrick *et al*., 2018; Klump and Gerhardt, 1992). One way to minimize competition for the acoustic space is made effectively by segregating the niche in its temporal and spectral dimensions (Both and Grant, 2012; Sinsch *et al*., 2012; Guerra *et al*., 2020, Lima *et al*., 2019). The temporal segregation of the advertisement calls can be fundamental for the constitution of large anuran assemblages, mainly in breeding areas

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where several species vocalize simultaneously (Drewry and Rand, 1983; Schwartz and Wells, 1983; Bertolucci and Rodrigues, 2002; Duarte *et al*., 2019).

The Yungas ecoregion is one of the most biodiverse environments in Argentina (Brown *et al*., 2006) harbouring up to 40 species of anurans (Lavilla and Heatwole, 2010). These subtropical montane forests are characterized by a steeped altitudinal gradient described by phytogeographic stratums (Grau and Brown, 2000). The anuran assemblages that inhabit the subtropical montane forest of the Parque Nacional Calilegua (PNC) within the Yungas ecoregion, was reported to present a wide range of temporal and spatial breeding patterns ranging from opportunistic to prolonged breeders (Vaira, 2002). However, these records of breeding activity were obtained based on regular monthly surveys lasting from 3 to 5 days carried out through active searches by visual and acoustic sampling (Vaira, 2002). The anuran assemblage of the PNC is composed by a few endemic species to the Yungas ecoregion and by numerous species with a wide distribution in Argentina and other South American countries (Lavilla, 2001; Vaira *et al*., 2017). In addition, a low number of studies aimed to describe and understand the complete acoustic breeding phenology over an entire year in neotropical anurans (Bertoluci and Rodrigues, 2002; Prado *et al*., 2005; Saenz *et al*., 2006). Therefore, there are still wide gaps of information about the daily and annual patterns of calling activity and the breeding acoustic phenology of the anuran species that conforms different assemblages inhabiting the Yungas forests.

A recent study suggests the use of PAM as an effective technique to monitor the species of anurans in the Yungas forests (Boullhesen *et al*., 2021). In addition, with the implementation of a PAM program, researchers were able to discover hidden behavioural insights of phenological activity, such as the nocturnal calling activity of a frog species

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inhabiting the Yungas forests, that was previously considered as a strictly diurnal species (Pereyra *et al*., 2016).

In this study, we describe the daily and annual patterns of calling activity of the anuran assemblages inhabiting the Yungas Andean Forests using PAM. Furthermore, we propose a new classification scheme for the acoustic breeding strategies used by different species of Neotropical anurans. Also, we aim to explore the occupation level of the acoustic communication channel and to determine the temporal overlap of the acoustic niche of this subtropical anuran assemblage.

MATERIALS AND METHODS

Study sites and data collection

A PAM was carried out for 12 months (from September 2017 to August 2018) along an altitudinal gradient in the PNC, being the most representative portion of the Yungas ecoregion in Jujuy province, Argentina. The PNC harbours the phytogeographic strata described for the Yungas forests as well as different environments where anurans breed (Vaira, 2002). The study was carried out in the three main forest types described for the ecoregion: Premontane Lowland Forests (400 - 700 m a.s.l.) which is a semideciduous environment with a marked seasonality, the understory consists of dense bushes, herbs, ferns and lianas; Lower Montane Forests (700 - 1300 m a.s.l.) dominated by evergreen trees such as *Juglans australis*, *Cedrella balansae* and *Enterolobium contortisiliquum*; the Upper Temperate Montane Forests (1500 – 2500 m a.s.l.) which is a primary old forest dominated by trees from Myrtacea family (Grau and Brown, 2000). The two upland forest types have markedly more moisture than the lower forests. Three automated recording units Song Meter 4 (Wildlife Acoustics Inc., Concord, Massachusetts), one per site were

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150 installed and programmed to record 3 minutes per hour (24/7) (Shirose *et al*., 1997;
151 Márquez *et al*., 2014). Recordings were done in MONO channel using in-built low noise
152 microphones and stored in 32GB SDXC Flash Cards in .WAV format. The recorders were
153 placed at 1.5 m above ground in three sites: Premontane Forest (PF) (23°45′16.84″ S;
154 64°50′59.35″ W, 650 m a.s.l.), at the edge of a permanent pond with an approximate area
155 of 1114 m^2. The Lower Montane Forest (LMF) (23°41'36.84"S; 64°52'5.04" W, 1125 m
156 a.s.l.), at the edge of a permanent stream and in Upper Montane Forest (UMF) (23°40
157 '28.56"S; 64°53'44.15" W, 1750 m a.s.l.), attached to a tree near temporary ponds.
158 Recorders were visited monthly to data download and battery replace. These locations
159 are representative to the breeding areas used by the anuran assemblage of the region
160 (Vaira, 2002).
161
162 *Data Analysis*
163 13,485 recordings were listened corresponding to one day per week (= 224.75 hours) from
164 the three study sites together throughout a year-round monitoring. Recordings were
165 inspected manually by a trained specialist in anurans call recognition of Yungas forests
166 (MB) in Raven Pro 1.5 (Bioacoustics Research Program, 2014) using a window type =
167 Hann, DFT size = 512 samples, and overlap = 50%. For the general description of the
168 acoustic phenology of the anuran species recorded, the monitored year was divided in two
169 seasons (six months each) marked by the regional climate as follows: A) spring-summer
170 season, corresponding to the period from September 2017 to March 2018. B) fall-winter
171 season, corresponding to the period from March 2018 to September 2018.
172 To describe the annual acoustic phenology, we used the classification of core
173 calling periods proposed by Lemckert and Mahony (2008). This considers the core calling
174 period for each species as the time-period containing > 90 % of the calling events. For

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these classifications we considered the species with a total of ≥ 50 calling events records only. With the data of the calling events per-day recorded throughout the year-round study we conducted a bottom-up hierarchical cluster analysis using vegan and cluster R packages. For this analysis euclidean distance and complete method were employed after correlation checking of the cophenetic distance obtained with the original data used (>0.90). This analysis was implemented in free software R.

To describe the daily and annual vocal activity of each species we adapted the classification proposed by Bridges and Dorcas (2000) as follows: 0 = no male vocalizing; 1 = one male vocalizing; 2 = multiple males vocalizing with the possibility of occasionally distinguishing single calls; 3 = multiple males vocalizing but unable to distinguish single calls. We considered each advertisement call detected from a recording as a "calling event", since we could not assign a distinct call to an individual. Circular statistics was employed to describe and analyse the daily calling patterns (Jammalamadaka *et al*., 2001; Pewsey *et al*., 2013). Rayleigh test was applied to explore whether the population of circular data, from which a sample is drawn, differs from randomness (Wilkie, 1983).

To explore temporal niche overlap in calling activity, we computed the Pianka (Pianka, 1973) and Czekanowski indices (Feinsinger *et al*., 1981) using the TimeOverlap program (Castro-Arellano *et al*., 2010; Guerra, 2020). The Czekanowski index or Proportional Similarity Index varies between 1 (widest amplitude of the niche where the population exploits the resources in proportion to their availability) and 0 (where the population specializes in the rarest state of a resource and skip the other items). Whereas the Pianka index can return values less than zero (allowing for a coexistence between species) or greater than one (promoting a competition between species).

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198 To characterize the use of the acoustic communication channel in anurans recorded,
199 the methodology proposed by Emmrich *et al*. (2020) was used according to their acoustic
200 calls features where:
201 Guild A = unmodulated simple call
202 Guild B = modulated simple call
203 Guild C = unmodulated pulsed call
204 Guild D = modulated pulsed call
205 Guild E = unmodulated pulsed multi-note call
206 Guild F = uniform modulated pulsed multi-note call
207 Guild G = non-modulated different multi-notes call
208 Guild H = modulated different multi-notes call
209
210 These guilds groups where previously visualized using clean calls from each species
211 recorded with the seewave package in R using a Hanning type windows, 75 % overlap
212 and 1024 sample size (Figure S1).
213
214 RESULTS
215
216 *Annual Calling Periods*
217 A total of 3318 calling events of anuran species were recorded in the three study sites
218 within the Calilegua National Park (Figure 1). We detected calling activity throughout
219 the entire year (Figure 1), with a minimum of one species vocalizing in the driest months
220 of July and August and a maximum of 16 species vocalizing simultaneously during
221 December (Figure 1). Most of the calls were recorded during the hottest and rainy period

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(spring-summer seasons), with peaks of calling activity during November, December, and January (Tables 1 and 2).

Boana riojana was the only species recorded throughout the year-round monitored and presented high records in the fall-winter period (Figure 1). Meanwhile, the rest of the species from Hylidae family were recorded calling over the spring-summer period (Figures 1-2). Most of the species from Leptodactylidae family where recorded calling at spring-summer periods, with the summer period having the highest core calling periods. However, *Pleurodema borellii* presented peaks of calling activity in the fall-winter period (Figure 1). The two toads of the genus *Rhinella* were registered calling during the early spring-summer period. Meanwhile *Melanophryniscus rubriventris* was recorded vocalising in the spring-summer, but also detected in the early dry-cold fall-winter period (Figure 1). The direct development-frogs from Craugastoridae family presented calling records concentrated in the spring-summer period, mainly during the summer season (Figure 1-2). The unique arboreal specie from Phyllomedusidae family (*P. boliviana*) presented calling records concentrated in the summer season (Figure 1-2).

Acoustic Breeding Strategies

The cluster analysis revealed five different acoustic breeding strategies (Figure 3): continuous breeders, prolonged non-seasonal breeders, prolonged seasonal breeders, prolonged non-regular breeders, and sporadic seasonal breeders.

A continuous breeding strategy was found in males of *Boana riojana*, who vocalized during all months of the year. A prolonged non-seasonal breeding pattern was observed in *Pleurodema borelli*, which started calling in spring-summer and continued through the fall-winter period. Prolonged seasonal breeders were clustered into two subgroups: prolonged-regular breeders called evenly spaced throughout the breeding

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247 season (spring - summer period), presenting many calling events records; prolonged non-
248 regular breeders had a calling activity spaced throughout the summer season. Sporadic
249 seasonal breeders were found in 9 species belonging to 5 different families, which called
250 sporadically during the spring-summer period only (Figure 3).
251
252 *Daily calling patterns*
253 Species of the family Bufonidae presented highly contrasting daily calling patterns.
254 Species of the genus *Rhinella* presented a mainly crepuscular and nocturnal calling
255 pattern; *R. arenarum* presented a peak of activity at 20:00 h, while *R. diptycha* vocalised
256 mainly between 20:00 h and 21.00 h (Rayleigh = 0.77; p = 0.0002; Rayleigh = 0.93; p =
257 0.0001) (Table 1, Figure 4). Meanwhile, *Melanophryniscus rubriventris* was mainly a
258 diurnal species, with peaks of vocal activity at 06:00 h and 18:00 h (Rayleigh = 0.52; p
259 <0.0001 (Table 1, Figure 4).
260 The species of the family Hylidae at the PF site recorded a mainly crepuscular-
261 nocturnal vocal activity, although sporadic calling activity was detected during the day.
262 *Boana riojana* was recorded at PF and at the LMF sites, at the PF site presented a mainly
263 nocturnal calling activity, with peaks of vocal activity at 01:00 h and 03:00 h; meanwhile,
264 at the LMF site, with a higher number of records, presented a mainly nocturnal calling
265 pattern, but also with diurnal vocalizations (Table 1, Rayleigh = 0.8; p < 0.0001).
266 *Dendropsophus nanus* presented a crepuscular-nocturnal vocal activity, with separated
267 activity peaks at 20:00 h, 21:00 h, and 05:00 h (Rayleigh = 0.65; p <0.0001). *Scinax*
268 *fuscovarius* presented a calling pattern mainly crepuscular and nocturnal, with a peak of
269 records at 22:00 h and 06:00 h, but also presented vocalizations during the day at 14:00
270 and 17:00 h (Rayleigh = 0.42, p <0. 0001). By the other hand, *S. nasicus* presented a more
271 sporadic and nocturnal vocal activity, with peaks at 22:00 h and 23:00 h (Rayleigh = 0.8,

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p = 0.005). *Trachycephalus typhonius* had a mainly crepuscular activity, with a peak of activity at 20:00 h, and was also recorded calling during the day at 14:00 h (Rayleigh = 0.59, p = 0.007).

The species of the family Craugastoridae presented a daily vocal pattern but was mainly crepuscular-nocturnal. *Oreobates barituensis* presented a sporadic pattern during the day with records of calls from 17:00 h to 20:00 h, with a peak of vocal activity at 05:00 h (Rayleigh = 0.5; p <0.0002) (Table 1, Figure 4). *Oreobates berdemenos* presented markedly crepuscular-nocturnal vocal activity with a peak of vocal activity between 05:00 h and 06:00 h but was recorded vocalizing continuously during the 24 hs of the day (Rayleigh = 0.3; p <0.0001).

Species of the family Leptodactylidae presented a mostly crepuscular-nocturnal daily vocal pattern, but records of calling activity were also detected during the day for some species. *Leptodactylus apepyta* began to vocalize at 19:00 h in the evening and peaked at 20:00 h and at 21:00 h (Rayleigh = 0.75; p <0.0001). *Leptodactylus macrosternum* presented a mainly nocturnal calling activity with a peak between 24:00 and 01:00 h but also was recorded calling during the daytime, frequently between 06:00 h and 08:00 h (Rayleigh = 0.59; p <0. 0001). *Leptodactylus elenae* called mainly at night, presenting peaks of calling activity at 22:00 h and at 01:00 h (Rayleigh = 0.68; p <0.0001). *Leptodatylus fuscus* presented a mainly nocturnal vocal activity, with sporadic peaks at 21:00 h and between 05:00 h and 06:00 h, with sporadic records during the daytime (Rayleigh = 0.66, p <0.0001). *Leptodactylus gracilis* was recorded even more sporadically, mainly at twilight, with a peak at 20:00 h (Rayleigh = 0.69; p = 0.0009). *Leptodactylus latinasus* presented a twilight-nocturnal vocal activity, beginning to call at 19:00 h, with extensive records during the last hours of the night and a peak of calling activity at 20:00 h (Rayleigh = 0.74; p <0.0001) (Table 1, Figure 4). *Phyllomedusa*

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297 *boliviana*, an arboreal species, presented a strictly nocturnal vocal activity, with records
298 of calls at 21:00 h and at 02:00 h, and a peak of calling at 22:00 h (Rayleigh = 0.81; p <0,
299 0001) (Table 1, Figure 4).
300
301 *Temporal niche overlap*
302 The annual temporal niche overlap, and the spring-summer season overlap of the recorded
303 species, was moderately high at PF site according to Pianka's index. According to the
304 Czekanowski's index, the use of the temporal acoustic space was equitable (Czekanowski
305 ~ 0.5) in the species assemblage recorded at the same site, both for the entire year and
306 during the highest records of vocal activity in spring-summer season (Table 2).
307 Meanwhile, the temporal niche overlap was lower in the LMF and UMF sites (Table 2),
308 according to the Pianka's index (Table 2). In addition, the time niche overlap during the
309 fall-winter season was moderate at LMF, according to the Pianka's index (Table 2).
310 According to the Czekanowski's index, a temporal niche overlap was found to be greater
311 than that expected by chance (coincident activity) in the spring-summer period in the
312 species that vocalize at the LMF site (Table 2).
313
314 *Calling guilds*
315 Six different calling guilds were recorded based on their advertisement calls features
316 (Table 3; Figure S1). *Leptodactylus apepyta*, was the only representative of the calling
317 guild "A"; *L. elenae*, *L. fuscus*, *L. latinasus*, *Physalaemus cuqui* and *Trachycephalus*
318 *typhonius*, were framed within the calling guild "B". *Rhinella arenarum* and *R. dypticha*
319 were part of the guild "D". *Oreobates barituensis* was the only representative of the
320 calling guild "E". *Boana riojana*, *Dendropsophus nanus*, *L. gracilis*, *Oreobates*
321 *berdemenos*, *Phyllomedusa boliviana*, *Pleurodema borellii*, *Scinax fuscovarius*, *S.*

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nasicus were part of the largest recorded group, the calling guild "F". *Leptodactylus macrosternum* and *Melanophryniscus rubriventris* formed the calling guild "G".

DISCUSSION

In this study, the calling phenology of anuran species is described at a fine timescale (hourly and daily) and quantitatively assessed along an altitudinal gradient in three Andean Montane Forest ecosystems of the Yungas ecoregion, within the PNC. This level of detail enabled us to propose a new classification scheme of acoustic breeding strategies according to the time spent by each species calling throughout a year.

Previous breeding strategies classification schemes were used to describe the breeding patterns of anuran species in the Calilegua National Park, following Duellman and Trueb (1986). Following this previous classification scheme only two breeding strategies were recorded for the entire species assemblage in this protected area (Vaira, 2002). Prado *et al*. (2005) described three reproductive activity patterns for a diverse anuran assemblage in a floodplain in the Pantanal region of Brazil. With the use of automatic recorders Saenz *et al*. (2006) were able to classify the anuran breeding activity patterns in: explosive breeders, winter breeders, summer breeders and continuous breeders depending on the core calling period recorded. Kopp *et al*. (2010) identified up to four distinct anuran reproductive patterns recorded by 13 visual encounter surveys in the Cerrado of Brazil. In this study, with the implementation of a PAM over an entire year we were able to identify five distinct breeding acoustic patterns and provide a novel, standardized classification framework, so that it can be tested in other ecosystems.

The great majority of the species recorded in this study showed a markedly seasonal breeding acoustic pattern, with their core calling periods centred during the spring-

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summer season in agreement with the warm and rainy season. These records were also reported by a previous study conducted on the same assemblage 20 years ago (Vaira, 2002). However, we now provide a detailed acoustic breeding phenology of the anuran species inhabiting three phytogeographical strata of the Yungas Andean Forest. The marked seasonal acoustic pattern might be related to the breeding behaviour present in these species that mainly use lentic waterbodies for their reproduction, with free-living tadpoles (Vaira *et al*., 2002; Pereyra *et al*., 2018; Boullhesen *et al*., 2019).

Strictly sporadic seasonal breeders were found in the families Bufonidae, Leptodactylidae, and Strabomantidae, with one to four calling events per month. The calling activity recorded for sporadic-breeding species in a tropical forest of Guyana lasted between one and three consecutive nights (Gottsberger and Gruber, 2004). The records of calls from explosive breeders were in coincidence with the warm and rainy period of the study. The calling activity of explosive breeders has been documented to correlate positively with temperature and rainfall cues in tropical anuran assemblages that use ephemeral ponds (Ulloa *et al*., 2019). Similarly, another study described the explosive breeders to call in the rainy season in the Pantanal of Brazil (Prado *et al*., 2005).

Prolonged seasonal breeders were the most representative groups in the study area. In another study along an altitudinal gradient of Brazil this reproductive pattern was also predominant among anuran species whose calling activity was recorded for 6 months (Arzabe, 1999). These temporal reproductive patterns agreed with others already reported for the Yungas forests (Vaira, 2002; Akmentins *et al*., 2015; Pereyra *et al*., 2018). The species of the family Leptodactylidae are mainly prolonged breeders, calling throughout the night and with sporadic calling activity during the day in representatives of the genus: *Leptodactylus*, *Physalaemus*, and *Pleurodema* (Vaira, 2002; Camurugi *et al*., 2017; Boullhesen *et al*., 2019). However, it should be noted that certain species of the family

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such as *Leptodactylus fuscus* were characterized as mainly nocturnal in other ecoregions (Lucas *et al*., 2008; Guerra *et al*., 2020), although they showed an extended pattern of calling activity in daylight time recorded by a PAM in the Yungas ecoregion (Boullhesen *et al*., 2019). Our work provides novel information about the acoustic phenology patterns of a recently described species, *L. apepyta*, calling in the summer season showing a crepuscular-nocturnal activity where males vocalize outside subterranean nests that they built near the edge of temporary ponds (Schneider *et al*., 2019).

The tree frog *Boana riojana* was the only continuous breeder recorded in the study area calling throughout every month of the year. Duellman (1970) suggested that the hylids of Central America reproduce continuously throughout the year if the environmental conditions are favourable. In addition, these records may, in turn, be linked to the characteristics of the monitored site. For example, the site LMF is characterized by abundant vegetation (evergreen forest) and a permanent mountain stream, providing optimal conditions for *B. riojana* to vocalise and breed throughout the entire year. In other species of this genus, a continuous breeding strategy has been suggested to correlate with adult male gravid and post metamorphic females' abundances recorded throughout a year of survey (Hiert and Moura, 2010). Previous research suggested that the members of the family Hylidae have a crepuscular-nocturnal vocal activity (Guerra *et al*., 2020). However, our PAM study showed that *B. riojana* also calls during daylight, thus suggesting a more plastic calling behaviour in this species. There are reports of diurnal movement in species of the genus *Boana* in temperate forests of Brazil (de Oliveira *et al*., 2016). Therefore, it is interesting to explore the vocal repertoire of *B. riojana*, to determine if these daytime vocalizations correspond to advertisements calls or other types of vocalizations, such as territorial interactions or rain calls (Toledo *et al*., 2015).

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The anuran assemblage recorded in this study presented a slight temporal acoustic niche overlap (time spent calling), mainly in the site with the highest diversity of species (PF). In addition, the temporal overlap of advertisement calls detected during the spring-summer period in the LMF site is remarkable. These results are in contrast with those reported for congeneric syntopic species that reproduce in permanent water bodies in the Cerrado savanna of Brazil (Guerra *et al*., 2020). The high diversity of species that compose the assemblages of the Yungas forests (Lavilla and Heatwole, 2010; Vaira *et al*., 2017), suggests that in places where several species reproduce simultaneously, the greatest diversity of calling patterns should be found to avoid being masked by others (Bertoluci and Rodrigues, 2002; Herrick *et al*., 2018; Klump and Gerhardt, 1992). The classification of advertisement calls of anurans, according to their spectral parameters in guilds, enables the comparison between groups of species to be faster and easier (Emmrich *et al*., 2020). This variety of acoustic strategies can be seen reflected in the calling guilds diversity detected in this study, mainly in the assemblage belonging to the PF site, with a total of five calling guilds recorded. Nevertheless, the calling guild with modulated pulsed multi-note calls was the most representative of the study, and unlike other guilds detected where there is a strong phylogenetic signal, this guild is made up of species from five different families. This observed pattern may conform with the Public Information Theory where anuran species with different phylogenetic relatedness elaborate advertisement calls with similar acoustics features (Danchin *et al*, 2004; Goodale *et al*., 2010; Sugai *et al*., 2021). In this sense, the anuran species belonging to different lineages could be using the same venue for information to determine the optimal conditions to breed. Thus, enabling an inadvertent social information resource available and driving the species to use similar acoustic traits (Danching *et al*., 2004; Goodale *et al*., 2010).

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The PAM employed in this study allowed us to describe in detail the acoustic reproductive patterns in an anuran assemblage in the mountain forests of the southern Yungas of north-western Argentina. This information made it possible to extend the previous knowledge regarding the calling activity of the species, contributing quantitatively to a better knowledge of a key aspect in the life history for each species recorded (calling activity), and to add new data for several secretive species.

In addition, it was possible to better characterize the variety of calling breeding strategies of the species recorded and, describe a standardized classification scheme to be tested in other ecosystems employing PAM method. In addition, we were able to access precise information on the temporal daily and seasonal acoustic distribution of the recorded anuran assemblage. This data is valuable and may be of great importance for implementing monitoring programs of anuran diversity in the Andean regions of South America.

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SUPPLEMENTARY MATERIAL

Supplementary material associated with this article can be found at <http://www-9.unipv.it/webshi/appendix/index.html> manuscript number 14050.

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688 TABLES

689 **Table 1.** Circular statistics for the anuran species recorded in the study sites. Mu = trigonometric moment; rho = length; sd = standard deviation;

690 cos = cosine; sin = sine; p = order; n = number of calling events; Rayleigh = Rayleigh uniformity test; *p* value = confidence value.

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Species	**mu**	**sd**	**rho**	**cos**	**sin**	**p**	**n**	**Rayleigh test**	**p value**
Boana riojana (PF)	6.08º	0.66º	0.38	0.38	-0.008	2	100	0.8	<0.0001
B. riojana (LMF)	6.25º	0.98º	0.15	0.15	-0.01	2	337	0.6	<0.0001
Dendropsophus nanus	0.51º	0.92º	0.15	0.02	0.15	2	167	0.65	<0.0001
Leptodactylus apepyta	4.13º	0.74º	0.33	0.29	0.15	2	50	0.75	<0.0001
L. macrosternum	5.14º	1.01º	0.17	0.17	0.02	2	127	0.59	<0.0001
L. elenae	6.49º	0.86º	0.14	0.14	-0.01	2	130	0.68	<0.0001
L. fuscus	8.89º	0.89º	0.21	0.15	-0.14	2	59	0.66	<0.0001
L. gracilis	6.9º	0.85º	0.08	0.08	-0.02	2	13	0.69	0.0009
L. latinasus	-0.4º	0.77º	0.74	-0.07	0.73	2	115	0.74	<0.0001

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Melanophryniscus rubriventris	12.43º	1.13º	0.05	-0.006	-0.05	2	67	0.52	<0.001
Physalaemus cuqui	5.77º	0.98º	0.02	0.02	0.001	2	212	0.61	<0.0001
Phyllomedusa boliviana	5.52º	0.64º	0.4	0.39	0.04	2	107	0.81	<0.0001
Pleurodema borellii	10.6º	1.35º	0.089	0.031	-0.08	2	96	0.39	<0.0001
Oreobates barituensis	13.85º	1.16º	0.18	-0.08	-0.016	2	31	0.5	0.0002
O. berdemenos	15.39º	1.53º	0.07	-0.05	-0.04	2	167	0.3	<0.001
Rhinella arenarum	4.22º	0.71º	0.43	0.39	0.19	2	12	0.77	0.0002
R. diptycha	5.93º	0.35º	0.77	0.77	0.01	2	6	0.93	0.001
Scinax fuscovarius	1.13º	1.3º	0.2	0.06	0.19	2	77	0.42	<0.0001
S. nasicus	4.23º	0.65º	0.6	0.54	0.27	2	7	0.8	0.005
Trachycephalus typhonius	5.38º	1.01º	0.079	0.078	0.012	2	13	0.59	0.007

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693 **Table 2.** Temporal acoustic niche overlap recorded in the study sites. Czekanowski index

694 (0-1); Pianka index (0-1).

Site	Period	Czekanowski	p-value	Pianka	p-value
PF	Annual	0.51	< 0.001	0.62	< 0.001
LMF	Annual	0.26	0.003	0.37	0.005
UMF	Annual	0.38	1.12	0.42	0.041
PF	Spring-Summer	0.51	< 0.001	0.61	< 0.001
LMF	Spring-Summer	0.31	0.003	0.4	0.007
UMF	Spring-Summer	0.38	1.12	0.42	0.041
PF	Fall-Winter	0.12	0.13	0.21	0.1
LMF	Fall-Winter	0.42	0.051	0.59	0.054
UMF	Fall-Winter	-	-	-	-

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Table 3. Calling guilds recorded along an altitude gradient within the Parque Nacional Calilegua, Argentina: permanent pond in the premontane forest (PF, 650 m a.s.l.), permanent stream in lower montane Forest (LMF, 1125 m a.s.l.), and upper montane forest (UMF, 1750 m a.s.l.). Total number of species recorded n = 19. Guild A = unmodulated simple call; Guild B = modulated simple call; Guild C = unmodulated pulsed call; Guild D = modulated pulsed call; Guild E = unmodulated pulsed multi-note call; Guild F = uniform modulated pulsed multi-note call; Guild G = non-modulated different multi-notes call; Guild H = modulated different multi-notes call.

Guilds	N° of recorded species	Percent	PF	LMF	UMF
A	1	5.26 %	1	-	-
B	5	26.31 %	5	-	-
C	-	-	-	-	-
D	2	10.52 %	2	-	-
E	1	5.26 %	1	1	-
F	8	42.10 %	7	2	1
G	2	10.52 %	1	-	1
H	-	-	-	-	-

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CAPTIONS TO FIGURES

Figure 1. Total number of calling events recorded for anuran species in the Parque Nacional Calilegua spanning the three sites together. Grey squares indicate calling activity. Dark squares indicate core calling periods.

Figure 2. Records of calling activity in the anuran assemblage of the Parque Nacional Calilegua. Black cells = maximum call events registered (3). Grey cells = medium calling events registered (2). Light cells = minimum callings events registered (1). PF = premontane forest; LMF = lower montane forest; UMP = upper montane forest.

Figure 3. Dendrogram showing the bottom-up hierarchical cluster analysis in the species recorded at the Parque Nacional Calilegua. Colours represent the five acoustic breeding strategies obtained.

Figure 4. Rose diagrams showing daily calling activity of recorded species in the study sites. Dotted lines = Kernel data distribution.

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726 Fig. 1

	2017						2018						
Species	September	October	November	December	Januar	Februar	March	April	May	June	July	August	Total
Boana riojana	44	237	211	214	152	51	22	4	82	1	35	66	1093
Dendropsophus nanus	8	16	14	36	51	35	14	1					175
Leptodactylus apepyta		5	16	33	19								73
L. elenae		10	32	48	45			2					137
L. fuscus			22	33	5								60
L. gracilis	2	3	4	1	1								12
L. macrosternum			31	51	28	15							125
L. latinasus	1	32	27	33	19	4							116
Melanophryniscus rubriventris			1	111	187	81							380
Oreobates barituensis	6	27	74	36	16	2	17						178
O. berdemenos	38	86	87	85	10		1	3	2	4			312
Pleurodema borellii		28	41	6	9	7	59	39					189
Phyllomedusa boliviana		6	24	40	36	5							111
Physalaemus cuqui		14	37	63	60	41	12						227
Rhinella dypticha	1	6											7
Scinax nasicus				12		4							16
Scinax fuscovarius	1	13	18	31	9	6							78
Trachycephalus typhonius			6	6	1								13
Total	101	483	645	803	648	301	125	49	84	5	35	66	3302

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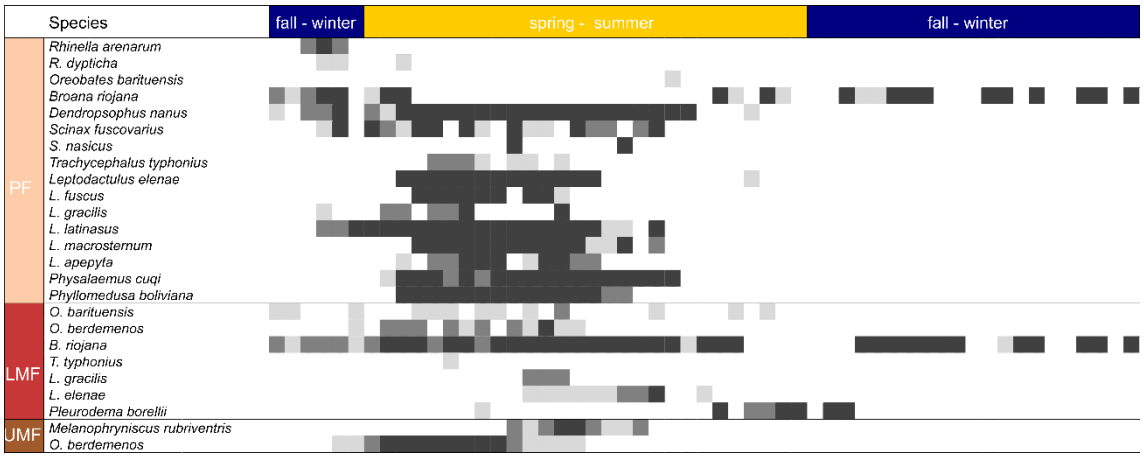
730 Fig. 2



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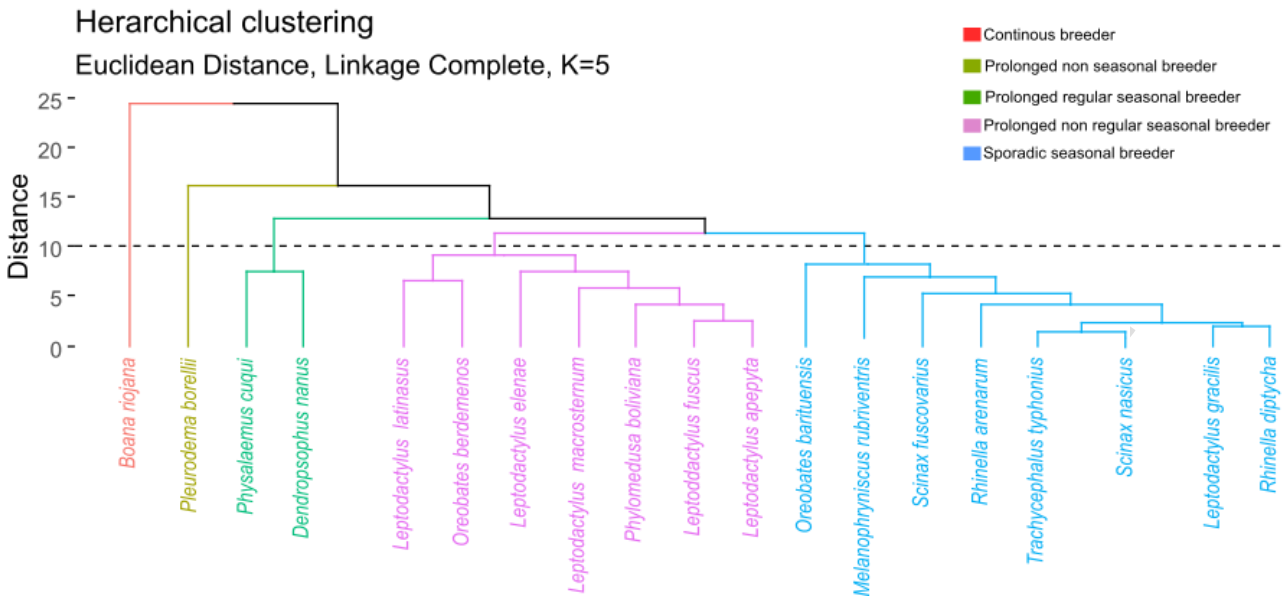
733 Fig. 3



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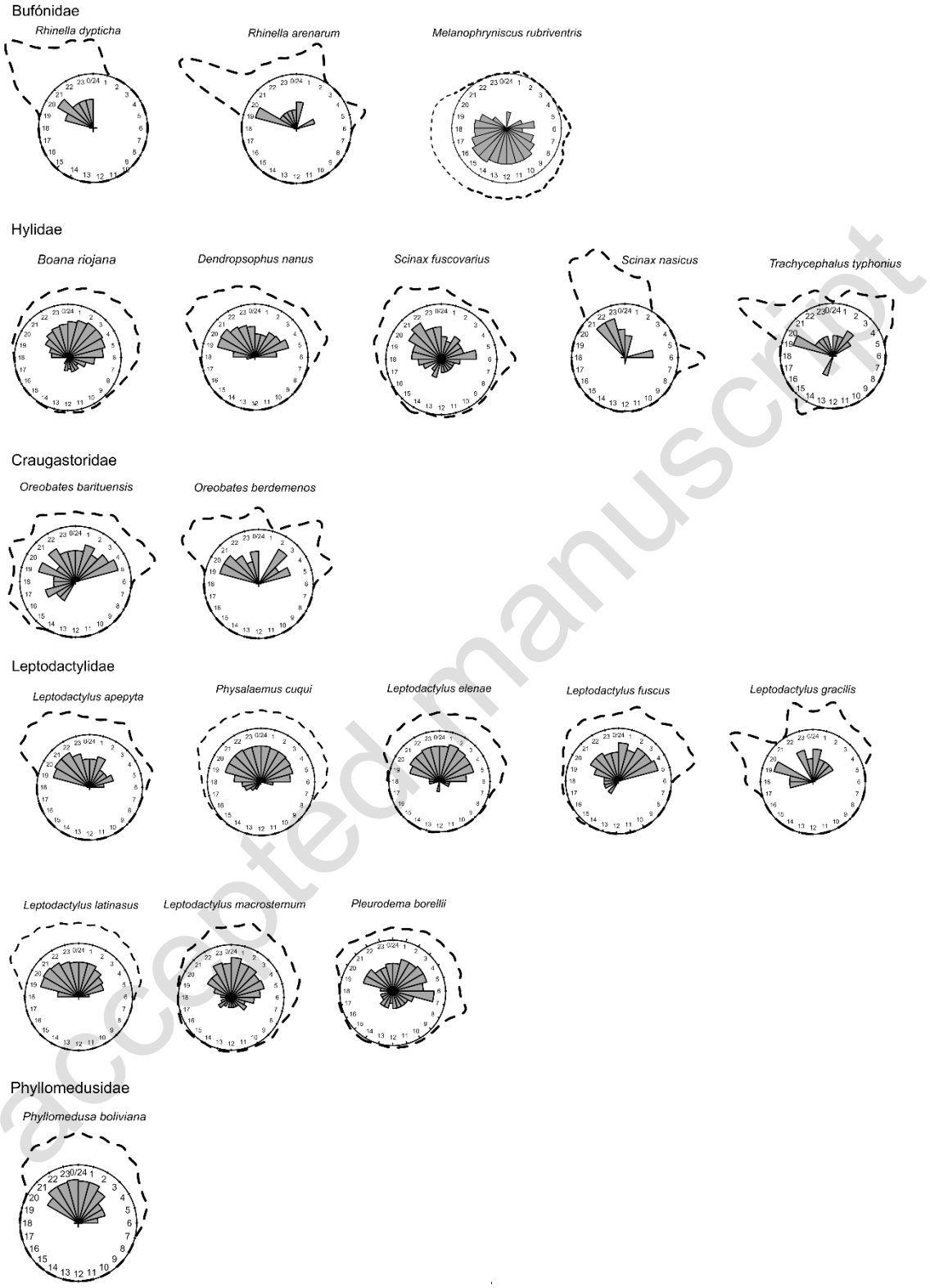
736 Fig. 4



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